

Chapter 6

Forest Insect–Natural Enemy Interactions



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6.1 Introduction

As illustrated in several other chapters of this book, “forest insects”, including those linked to woody plants growing outside the forest environment *stricto sensu* (cities, field margins, hedgerows, river banks, roads, railway tracks, etc.), play various ecological and economic roles (pests, biocontrol agents, pollinators, recyclers of nutrients, key components of trophic webs, etc.). Often, the role of natural enemies in intricate food webs can be extremely complex and may change according to the presence and prevalence of other food web components. For example, the interactions of two prey species occupying the same niche and facing a common predator could result in a competitive advantage for one of the two prey species, if it suffers less damage from the predator (see Sect. 6.3).

Although the forest environment provides very specific habitats for natural enemies and their prey (see Sect. 6.4), in many respects natural enemies of forest insects are not different from species attacking prey or hosts in other habitats. Accordingly, ecological processes and behavioural traits such as specificity, prey/host location and exploitation, intra- and interspecific competition, multitrophic interactions, coevolutionary dynamics, can be found in any natural enemy in any habitat. Consequently, when relevant examples of these processes in forest natural enemies are not available, examples illustrating particular features of the complex relationships between insects and their natural enemies will sometimes be drawn from non-forest ecosystems.

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6.2 Natural Enemies

Any organism feeding on another species or group of species during at least one developmental stage can be described as a “natural enemy”, a category to which predators, parasitoids and pathogens attacking forest insects obviously belong. To extend the label more widely, it could be argued that herbivores are natural enemies of the plant species they feed upon (see Sect. 6.3. Food webs). The categories: *predators* (mostly small mammals, birds, arthropods) and *parasitoids* (insects), *nematodes*, and *pathogens* (bacteria, fungi and viruses) are briefly discussed below. For comprehensive syntheses regarding natural enemies of insects in general, see Hajek and Eilenberg (2018) and Jervis (2012).

6.2.1 Predators

Predators kill, and feed on, live prey. Each individual consumes several prey during its development. Some species are predatory only at a given life stage. The adults of the common green lacewings (*Chrysoperla carnea*: Neuroptera, Chrysopidae) feed on pollen but their larvae consume a wide range of prey (aphids, scale insects, moth or butterfly eggs or larvae) (Huang and Enkegaard 2010), as well as extrafloral nectar (Limburg and Rosenheim 2001). Conversely, all life stages of the Monotomid beetle, *Rhizophagus grandis*, feed on the immature stages of the bark beetle *Dendroctonus micans* (Grégoire 1988).

Many predator species are *polyphagous* (attacking several families) or *oligophagous* (attacking several genera within one family). Small mammals and birds are notoriously polyphagous, shifting diet according to circumstances, even alternating between predation and herbivory. The white-footed mouse, *Peromyscus leucopus*, an important predator of the spongy moth, *Lymantria dispar*, is known to feed primarily on acorns and to expand its diet to include spongy moth pupae when they become locally available (Elkinton et al. 1996). The Clerid beetle, *Thanasimus formicarius*, is a good example of an oligophagous predator. It is restricted to Scolytinae but attacks at least 27 species within this sub-family (Warzée et al. 2006). Some predators are *monophagous* (feeding on a few, or even one species within one genus). For example, *R. grandis* is known to attack only one species: *Dendroctonus micans*, but there are only very few such cases (Dohet and Grégoire 2017).

A wide variety of organisms exhibit a predatory life style. Wegensteiner et al. (2015) listed 218 species recorded as predators of bark- and ambrosia beetles in Europe and North America, including 168 insect species belonging to 4 orders and 21 families, 40 mites and ten woodpecker species. Among the insects, predators belong to many families, including the Carabidae, Cleridae, Cucujidae, Histeridae, Monotomidae, Nitidulidae, Staphylinidae, Tenebrionidae, Trogossitidae, and Zopheridae.

Dipteran predators most commonly belong to the families Asilidae, Dolichopodidae, Empididae, and Lonchaeidae.

A review of forest pest control by vertebrate predators is provided by Buckner (1966). Small mammals have been observed to exert strong predatory impacts, in particular on ground dwelling life stages (sawfly and moth pre-pupae and pupae). Two shrews, *Sorex cinereus cinereus* and *Blarina brevicauda talpoides* and a deer mouse, *Peromyscus maniculatus bairdii* are important predators of the European pine sawfly, *Neodiprion sertifer* in Canada (Holling 1959a). *Peromyscus leucopus* is recognised as the major mortality factor regulating low-density populations of the Spongy moth in the eastern US (Elkinton and Liebhold 1990; Liebhold et al. 2005). Various species of birds exert strong pressure on Lepidoptera (Seifert et al. 2015) and scolytine beetles (Karp et al. 2013). Woodpeckers (Picidae) play an important role in the population dynamics of the Emerald Ash Borer, *Agrilus planipennis* (Coleoptera, Buprestidae) in North America (Jennings et al. 2016).

6.2.2 Parasitoids

Parasitoids differ from true parasites (e.g. flatworms, *Tenia* spp.) in that they eventually kill their hosts at the end of their own development. Even though a host may be infested by a developing parasitoid, the hosts survive and can sometimes produce progeny before they are killed. There are internal (endo-), and external (ecto-) parasitoids.

Each parasitoid larva consumes one single host during its development, but, in gregarious parasitoid species, several parasitoid larvae can share the same host. Adults may also exert an impact on their hosts via *host-feeding*, during which they puncture the host cuticle and feed on its haemolymph. As described above for predators, parasitoids can be monophagous, oligophagous or polyphagous. An example of a monophagous parasitoid is *Avetianella longoi*, an Encyrtid parasitoid of the Eucalyptus longhorned borer in California, USA. This parasitoid was successful in controlling *Phoracantha semipunctata* (Paine et al. 1993). But when *Phoracantha recurva* (in the same genus) was introduced into California, *A. longoi* was not effective in attacking or controlling the new pest.

Parasitoids are generally classified as either *idiobiont* or *koinobiont*. The *idiobionts* attack mostly hidden hosts (e.g. xylophagous larvae feeding on the sapwood within trees or branches), which are first paralysed, after which one or several eggs are laid on or near (but not within) the host (Fig. 6.1). The *koinobionts* are generally endoparasitoids. The host is often immature and continues to develop, which allows the host to grow and provide a larger food supply to the parasitoid larvae. To take advantage of the increased resource from a larger host, some parasitoids delay development until the host pupates, even if oviposition occurred in the host egg. However, the koinobiont strategy also imparts some important constraints. Because the host is still active (as opposed to the paralysed hosts of the idiobionts), it has the opportunity to defend itself by encapsulating the eggs with melanocytes (see also Sect. 6.5.2).

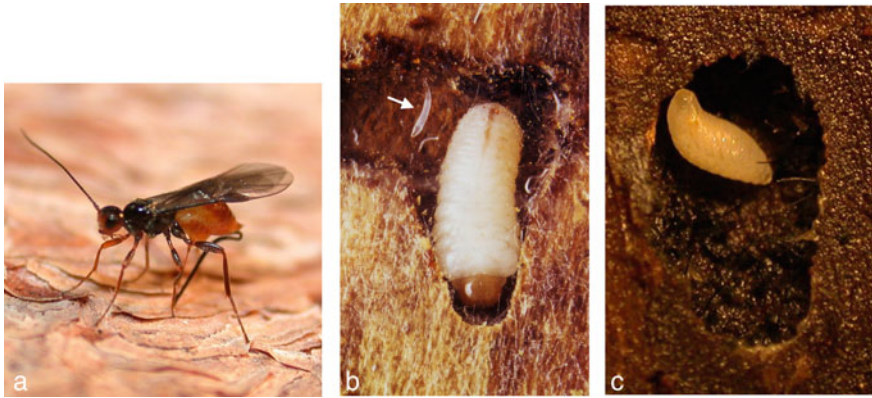


Fig. 6.1 *Coeloides bostrichorum* (Hymenoptera, Braconidae). a. female ovipositing through the bark; b. egg (arrow), next to a paralysed *Ips typographus* larva; c. mature parasitoid larva ready to spin a cocoon; the remnants of the host are not visible. Photos: Courtesy of Evelyne Hougardy

Also, when the host is more active it is susceptible to predation, which would kill the parasitoid larvae as well as the host.

Females of some gregarious species lay several eggs in each host while others lay one single, *polyembryonic* egg which, after many divisions, will produce up to several hundred clonal larvae. In some species with polyembryonic eggs there is larval caste differentiation: short-lived “soldier” larvae hatching first and roaming the host in search of competitors to destroy, and reproductive larvae that hatch later and become reproductive adults (Cruz 1981; Giron et al. 2004). Some species are *pro-ovigenic*: the females emerge with a complete egg load that will not increase. Others are *synovigenic* and have only a limited set of eggs upon emergence and need to feed (e.g. nectar, pollen, host-feeding) in order to develop additional eggs. For example, females of *Scambus buoliana* (Hymenoptera, Ichneumonidae), a parasitoid of the European pine shoot moth, *Rhyacionia buoliana* (Lepidoptera, Tortricidae) must host-feed or feed on pollen to increase longevity and fecundity (Leius 1961; 1963). Similar results have been reported for hymenopteran parasitoids of bark beetles (Mathews and Stephen 1997; Hougardy and Grégoire 2000). When food or hosts are scarce, synovigenic parasitoids can resorb their eggs in order to redirect resources to other physiological functions and resume oviposition when resources are available again.

Many families of Hymenoptera are primarily or exclusively parasitoids, including the Ichneumonidae, Braconidae, Torymidae, Chalcididae, Eurytomidae, Pteromalidae, Encyrtidae, Eulophidae, Trichogrammatidae and Aphelinidae. There are also parasitoids among the Diptera (e.g. the Bombyliidae and the Tachinidae) and the Coleoptera (e.g. some Staphylinidae, Bothriideridae, Carabidae and Meloidae). A comprehensive review of the biology and ecology of parasitoids is provided by Godfray (1994).

There are multiple forms of parasitism (see Box 6.1).

BOX 6.1—Forms of parasitism by insect parasitoids

Primary parasitoids. Species that develop on non-parasitoids.

Hyperparasitoids. (secondary, tertiary parasitoids). Develop on other parasitoids. There may be more than one level of hyperparasitism in a system. Some hyperparasitoids oviposit directly in or on a primary parasitoid, others oviposit on or in the host, and their larva search for larval primary parasitoid hosts.

Multiparasitism. Two or more species of primary parasitoids which concurrently attack the same host. This phenomenon creates a high level of interspecific competition. Sometimes, multiparasitism is obligatory (see cleptoparasitoids).

Superparasitism. Several parasitoids of the same species can oviposit in or on the same host.

Autoparasitism. Some species lay female eggs in unparasitized Sternorrhynchan hosts but lay male eggs in the immature parasitoids (of the same or another species) already present inside of the host.

Cleptoparasitoids. “Host stealers”. These species, unable to paralyze a host themselves, are obligatory multiparasitoids. They only select hosts already parasitised by another species.

6.2.3 *Nematodes and Pathogens*

Nematodes and entomopathogenic viruses, bacteria, fungi and microsporidia are widely present and active in the forest and, similarly to insect parasitoids and predators, some of them are mass-produced and released as biological control agents. Reviews on the use of pathogens against insects have been published by Lacey and Kaya (2007), Lacey et al. (2015), Lacey (2016) and Hajek and van Frankenhuyzen (2017). Nematodes were reviewed by Poinar (1975, 1991) and Kaya and Gaugler (1993).

Nematodes (roundworms) are long and thin worms, living in moist environments, including the soil or the body of plants or animals. The adults of some *Gordius* species (horsehair worms, Mermithidae) that parasitise locusts, crickets or roaches measure 30–120 cm. Other nematodes are microscopic.

There are many known cases of nematodes infesting forest insect pests. For example, *Deladenus siridicola* (Neotylenchidae), has been introduced to many parts of the Southern Hemisphere to control the Eurasian and North-African woodwasp, *Sirex noctilio*. This nematode can sterilize female woodwasps (see also

Sect. 6.3). Also of particular interest here are the so-called “entomophilic” or “entomopathogenic” nematodes (Steinernematidae and Heterorhabditidae), which are entomopathogenic because of their association with mutualistic bacteria in the genus *Xenorhabdus*. The bacteria are introduced by the nematodes into the body of a living insect, kill the host and feed and multiply on its dead body. The nematodes feed on the bacteria which also produce antibiotics that inhibit the growth of competing bacteria. The bacteria can also attack other nematodes that compete with their own associates. For example, *Xenorhabdus bovienii*, a symbiont of *Steinernema affine* can directly attack its competitor, *S. feltiae* and thus reduce competition by this latter nematode species (Murfin et al. 2019). *Steinernema* spp. infest the soil-inhabiting life stages of various beetles, moths and sawflies. *Heterorhabditis* spp. attack the soil-dwelling larvae of various scarabeids and weevils. Some *Steinernema* species are “ambushers”, waiting for an insect to cross their path. Other nematodes (e.g. *Heterorhabditis* spp.) are “cruisers”. They move actively in the soil, using semiochemicals and vibrations to locate prey.

Bacteria are unicellular organisms 0.5–5.0 μm long, protected by a membrane and a cell wall, with a single, naked circular DNA chromosome. The bacteria reproduce by fission, but they can also produce spores. They occur in many shapes (spherical, linear, spiral-shaped), and they are extraordinarily abundant everywhere in the world. Some are saprophytes (feed on decaying plant matter), some are symbiotic, and others are pathogens of plants and animals. A common bacterial entomopathogen is *Bacillus thuringiensis*, with distinct subspecies infecting different insect orders. The bacteria produce *sporangia*, containing a spore and a *crystal*. When swallowed by an insect, the crystal is dissolved in the alkaline conditions of the gut, and the *protoxin* within, activated by the gut’s enzymes, attaches to the gut wall, creating pores through which the bacteria invade the host’s body.

Fungi Many species of fungi infect insects, in particular among the orders Entomophthorales (e.g. *Entomophthora* spp.) and Hypocreales (e.g. *Beauveria* spp. and *Metarhizium* spp.). Pathogenic fungi start colonizing a new host via a spore attaching itself to the cuticle. The spores germinate and produce hyphae that enter the host through the cuticle, often at a thinner location (ventral surface, spiracle, sensilla, or joints between appendices or segments). In some species of fungal pathogens, the hyphae start covering the host’s body before penetration occurs. Penetration is facilitated by enzymatic processes and mechanical pressure. Once inside the host, the fungus most often kills the host and colonizes its entire body. In many cases, the host’s behavior is manipulated by the fungus, so that it dies in an exposed position, from which the fungal spores will have improved opportunities to reach a new host. There are various forms of fungal spores, some short-lived that allow direct contamination of another insect, others more resistant to climate and long-lived.

There are numerous examples of fungi attacking forest insects, e.g. *Beauveria bassiana* colonizing bark beetles, *B. brongniartii* attacking cockchafer, and *Entomophaga maimaiga*, found since 1989 to cause important epizootics among North American populations of *Lymantria dispar*. A comprehensive review of the parasitic fungi has been provided by Boddy (2016).

Microsporidia are unicellular organisms previously classified among the Protozoa, but which now belong to their own phylum, the Microspora. They live as obligate parasites within the cells of a large array of animal hosts, primarily arthropods, including insects (e.g. bees, locusts, bark beetles, Lepidoptera), but also other organisms such as nematodes and man. They can alter the behavior of their hosts, seriously impair, or kill them. They produce spores which are ingested by a new host and, once inside its digestive tract, extrude a long *polar tube* to inject themselves directly into a host cell. Examples of microsporidia infecting forest insects include *Nosema* species infecting bark beetles and the *Nosema*, *Vairimorpha* and *Endoreticulatus* spp. infecting forest Lepidoptera. These organisms affect not only their hosts, but also the endoparasitoids infesting these hosts. It has consequently been proposed that they can exert an important influence on the population dynamics and life cycle of these different insects.

Viruses are very small particles (*virions*), ca 10–150 nm long, which replicate inside the living cells of other organisms including bacteria, fungi, animals or plants. They consist of genetic material (RNA or DNA), surrounded by a protein shell, the *capsid*, itself sometimes encased in a lipid layer. They reach a new host via contaminated food or water or are spread by vectors (e.g. insects). Among the entomopathogenic viruses, the most common are the *baculoviruses* (Baculoviridae), which have double-stranded DNA. Some baculovirus species infect the larvae of moths (e.g. *Lymantria dispar*; *L. monacha*) and sawflies (e.g. *Gilpinia hercyniae*; *Neodiprion sertifer*). Baculoviruses may be protected before they enter the host body by a protein inclusion body, resistant to desiccation, light etc. Among the Baculoviridae, the *polyhedrosis viruses* are protected by polyhedral inclusion bodies that may contain many virions. There are *nuclear polyhedrosis viruses* (NPVs), replicating in the cells' nuclei, and *cytoplasmic polyhedrosis viruses* (CPVs), replicating in the cells' cytoplasm. The virions of the *granuloviruses* (GVs) are each protected by a rounded, smaller inclusion body.

A review of the use of pathogens as biopesticides has been recently published by Senthil-Nathan (2015).

6.3 Food Webs

Each host plant, herbivore, parasitoid, predator and pathogen is part of an often very complex *food web*. Each natural enemy can feed on several target species, and is itself attacked by other organisms, which are often prey for other species. The successive trophic levels that constitute a food web start at the primary producer (host-plant) level, the organisms in each additional level feeding on those of the one below (Price et al. 1980), with top predators occupying the highest level (Rosenheim 1998). This structure is further complicated by horizontal competitive or aggressive relationships between species sharing any given trophic level. For example, there is evidence that the larvae of the pine sawyers *Monochamus carolinensis* and *M. titillator* (Coleoptera, Cerambycidae) exert *intraguild predation* (predation on other

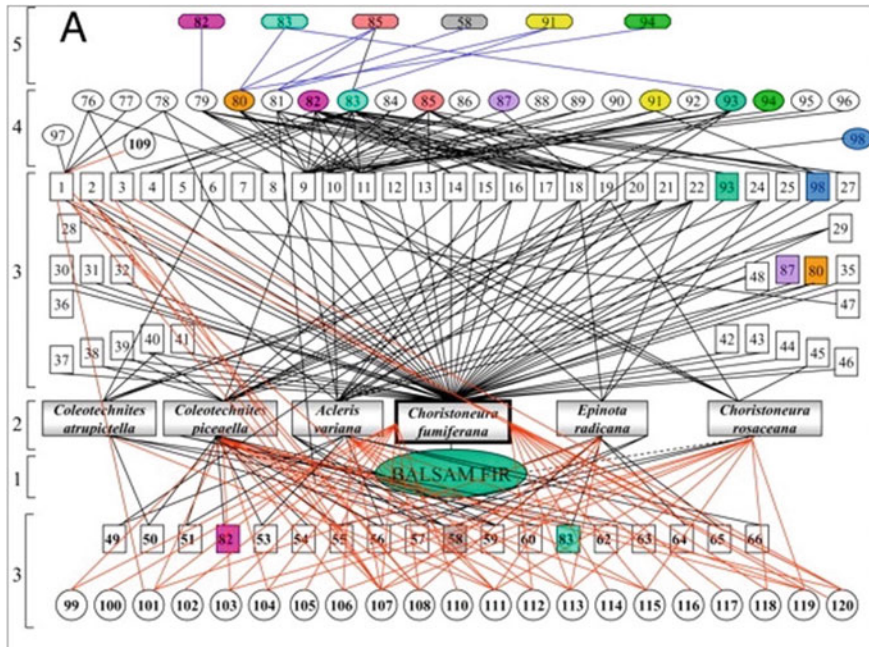


Fig. 6.2 A global food web established after ten years (1983–1993) of sampling in three balsam fir (*Abies balsamea*) stands infested by the spruce budworm, *Choristoneura fumiferana* in New Brunswick. Primary parasitoids are represented by squares, secondary parasitoids by ovals, tertiary parasitoids by octagons, and entomopathogens are represented by circles connected by red lines to hosts. The brackets and numbers on the far left identify trophic level. Vertebrate and invertebrate predators were not included in the study and therefore are missing in the figure. From Eveleigh et al. (2007)¹

species sharing the same ecological niche) on bark-beetle species also feeding on phloem and sapwood (Dodds et al. 2001; Schoeller et al. 2012).

An existing food web can exert an adverse impact on exotic natural enemies introduced for classical biological control (see Sect. 6.6.5). When the ichneumonid parasitoid *Olesicampe benefactor* was introduced into Canada for the biological control of the European larch sawfly, *Pristiphora erichsoni*, it became a prey item of a local hyperparasitoid, the ichneumonid *Mesochorus dimidiatus*, which greatly reduced its impact (Ives and Muldrew 1984).

Figure 6.2 shows a complex global food web, suggesting the various feedback loops, negative and positive, that can arise from the interactions between organisms at the various levels. The primary hyperparasitoids (“secondary parasitoids” in the figure’s legend) alleviate the burden of the parasitoids (“primary parasitoids”) on the central species, *C. fumiferana*, and the secondary hyperparasitoids restore some of the impact of the parasitoids.

¹ Permission requests: <http://www.pnas.org/page/about/rights-permissions>.

Figure 6.2 also helps to understand the concept of *apparent competition*, which occurs when, at a given trophic level, several species share natural enemies. The species that produce more shared enemies are predicted to have a higher competitive impact on the other species at the same trophic level. This has been experimentally observed, e.g. by the artificial removal of herbivore species. Morris et al. (2004), studying a community of leaf-miners in a moist tropical forest in Central America, found that it was inhabited by 93 insect species from various orders, attacked by 84 species of hymenopteran parasitoid. After removing two of these leaf-mining species (by uprooting their specific host plants), the remaining species experienced significantly less parasitism by the parasitoids that they shared with the removed species. Conversely, increased but temporary, availability of an alternate food source can result in a larger reservoir of natural enemies, and increased predation on an insect pest after the alternate food has decreased in availability. Over a ten-year period in Massachusetts, Elkinton et al. (1996) recorded a negative correlation between spongy moth (*Lymantria dispar*) abundance and the abundance of an important predator, the white-footed mouse, *Peromyscus leucopus*, and a positive correlation between acorn crops (a basic food for *P. leucopus*) and population density changes in the mouse. So, *L. dispar* outbreaks, synchronised over large areas, appear lag correlated with periodical oak masting patterns (Liebhold et al. 2000).

Natural enemies in a food web can make complementary prey choices. Singer et al. (2017) censused the lepidopteran larvae in the canopies of eight deciduous tree species in northeastern USA after they excluded birds and reduced ant density. They found that birds selectively chose large generalist caterpillars while ants preferred the smaller host specialists, and that the combined impacts of the two types of predators were additive. Non-native species can alter food web dynamics and reduce the impact of biological control agents. For example, the bark beetle *Ips grandicollis* has invaded Australia and when it colonizes dying *Pinus* spp. it introduces the fungus *Ophiostoma ips* to this resource. The nematode *Deladenus siricidicola* is mycetophagous for part of its life cycle, feeding on *Amylostereum areolatum* which is the fungal symbiont of *Sirex noctilio*. The rest of its life cycle, *D. siricidicola* is parasitic on *S. noctilio* and this nematode is an important component of management programs for *S. noctilio* throughout the southern hemisphere. The presence of *O. ips* in dead pine reduces the availability of *A. areolatum* which in turn reduces the performance of *D. siricidicola* as a biocontrol agent for *S. noctilio* (Yousuf et al. 2018).

A striking example of a cascade of changes in the tritrophic interactions in a food web is provided by a study by Palmer et al. (2008) on the ant-acacias *Acacia drepanolobium* in a Kenyan savannah. The trees have extrafloral glands that produce nectar which attracts several ant species, and the tree provides domatia, small chambers that some of these ant species use as shelters. The ants protect the trees against large herbivores and woodboring insects. After ten years of exclusion of these herbivores, the trees had reduced their investment in nectar production, which had led to a shift in the dominant ant species towards a species nesting in Cerambycid galleries instead of domatia. This in turn resulted in higher colonization by woodborers and higher tree mortality.

6.4 The Forest Environment and Natural Enemies

The forest environment is generally favourable to many animal species because it is (i) *long-lived*, (ii) *diversified* and (iii) it often *extends over large or very large areas*.

- (i) *Long-lived*—in strong contrast to insect life cycles which typically range from a few weeks to two or three years, most forest types remain in place for decades or centuries, with even “permanent” coverage in the case of unmanaged forests or of stands managed by selection cutting and natural regeneration. Even short rotation coppices (stands of willows or poplars harvested every 2–5 years for biomass) provide a longer lived (more stable?) habitat than agricultural land.
- (ii) *Diversified*—one hectare of rainforest may contain several hundred tree and higher plant species vertically distributed in multiple layers. Even monospecific, even-aged plantations show a surprising level of complexity (Brockerhoff et al. 2008). For example, a survey of five 60–80 year old spruce plantations in Belgium identified 53 species of herbaceous plants belonging to more than 20 families, sometimes in large numbers in clearings and gaps. These plants provide nectar and pollen to local synovigenic parasitoids that need to feed as adults in order to produce more eggs or to keep their existing load (Hougaard and Grégoire 2000). This high diversity of plants favours a high diversity of natural enemies feeding on multiple hosts, prey or other sources, and provides a large choice of habitats.
- (iii) *Extends over large or very large areas*—forests cover ca. 4 billion ha in the world, i.e. 31% of the total land area (Keenan et al., 2015), with some extremely large, continuous coverage, and also with very small plots. The small forests are often located side by side, forming larger blocs with, from an insect’s standpoint, no or little distinguishable boundaries between the individual units. The largest forest plantation in Europe (one million ha), the pine *Forêt des Landes* close to Bordeaux in south-western France, belongs largely (92%) to 58,500 private owners, half of which own less than 1 ha (Pottier 2012), and yet pests and natural enemies roam the whole massif freely.

Several other forest attributes are important to natural enemies:

- *Forest fragmentation* (the extent and grain of the mosaic of cleared and forested land) has been shown to influence the parasitism rate of the forest tent caterpillar (*Malacosoma disstria*) by four dipteran parasitoids in Alberta, Canada. According to their relative body sizes (correlated to their dispersal capacity), the four species performed better at different levels of fragmentation because larger flies could fly further (Roland and Taylor 1997). Cronin et al. (2000) showed with mark-release-recapture experiments that the clerid predator *Thanasimus dubius* has a higher mobility than its prey, the bark beetle *Dendroctonus frontalis*. The radius containing 95% of the recaptured insects was 5.1 km for the predators, and 2.3 km for the prey, allowing the predators to forage in distant patches when experiencing patches of local prey extinction. Using examples taken from the host-parasitoid literature, Cronin and Reeve (2005) further argue that, because of local extinction

of either parasitoid and host or predator or prey, their interactions need to be studied at a scale sufficiently large to include the metapopulation level. From a review of theoretical work regarding the impact of habitat loss and fragmentation on predator–prey relationships, Ryall and Fahrig (2006) list a series of criteria that should be considered in further studies: prey and habitat specificity, extinction rates of prey-only and predator–prey patches, prey emigration rates from prey only vs. predator–prey patches.

- *Tree species composition* also has an impact on natural enemies. Because it needs the thick bark of pine for pupation and can less easily pupate in the thinner bark of spruce (Fig. 6.3), the oligophagous predator of Scolytinae, *Thanasimus formicarius*, was significantly more abundant in stands where spruce was mixed with pine in North-Eastern France than in pure spruce stands, and this higher frequency was associated with lower populations of the bark beetle *Ips typographus* (Warzée et al. 2006).
- *Forest type* also influences the abundance and impact of natural enemies. For example, Liebhold et al. (2005) observed that the abundance of *Peromyscus* sp. mice in Wisconsin and the level of control they exerted on the gypsy moth were higher in mesic sites than in urban and xeric forest types.

Forest can serve as *reservoirs of natural enemies*, spilling out towards cultivated areas, especially when, as measured by Cronin et al. (2000), natural enemies have a higher mobility than their prey. From a systematic literature review encompassing

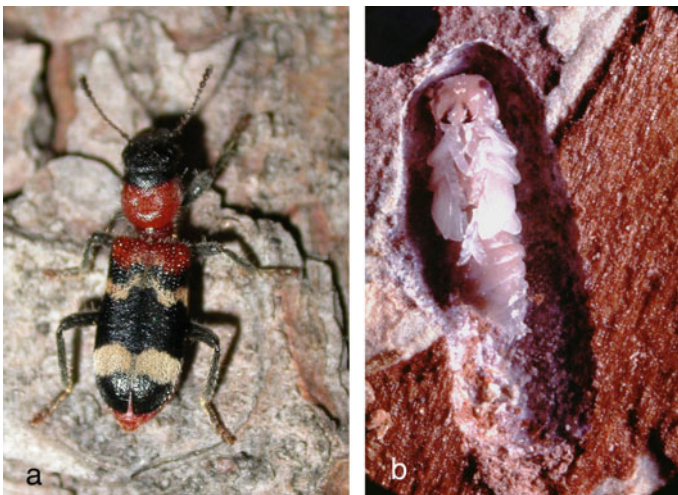


Fig. 6.3 *Thanasimus formicarius*. a. An adult roaming the bark surface, either for oviposition below a bark scale, or hunting for adult *Ips typographus*. b. A pupa in its niche inside the bark. If the bark is thinner than 6 mm, pupation cannot occur, and the mature larvae leave the tree. Figure 6.3a: Courtesy of Nathalie Warzée; Fig. 6.3b: Jean-Claude Grégoire

158 studies, Boesing et al. (2017) concluded that in tropical areas, at least, avian predators that exert significant control on agricultural pests depend on native forests. For example, Karp et al. (2013) observed an increased abundance of avian consumers of the coffee berry borer beetle (the bark beetle *Hypothenemus hampei*), as well as lower infestation levels in Costa Rican coffee plantations established in more forested landscapes. *Natural enemy spillover*, however, can occur in the other direction, from cultivated landscapes to natural forests. Frost et al. (2015) used interception traps to quantify spillover of generalist predatory wasps (*Vespula* spp., Vespidae) and of 106 species of more specialized hymenopteran parasitoids of lepidopteran caterpillars between native forest, dominated by Nothofagaceae, and exotic *Pinus radiata* plantation forest in New Zealand. They found that spillover of both generalist and specialist predators was directed from plantation to native forest, with a greater trend among generalists. They interpreted this as the result of a higher productivity of caterpillars in the plantation forest. This hypothesis was verified for the *Vespula* spp. but not for the specialist parasitoid wasps, by selectively suppressing the caterpillars in the plantation forest plot by spraying a formulation of *Bacillus thuringiensis* var. *kurstaki*, which affects Lepidoptera but no other insect orders.

6.5 Predator–Prey Relationships

In this section and unless specified otherwise, predators, parasitoids and pathogens are all referred to as predators and prey and all host species as prey.

All predators need to locate, overcome and consume their food, and optimally exploit those species that are currently available. They rely for prey location on various stimuli: including visual cues, semiochemicals, sound, vibration, and heat. In many cases, the prey's host-plant is also involved in attracting or maintaining predators: they emit semiochemicals, provide alternate food (e.g. from extra floral nectaries), or offer shelters (the domatia of ant-acacias, see Sect. 6.3). Finding a prey, however, is only the beginning of a whole sequence of events. For example, parasitoids that oviposit in living hosts need to increase the survival chances of their eggs, specialised predators feeding on rare prey need to optimise their consumption, pathogens need to colonise their host and to propagate to other hosts. At a higher level, the population dynamics of predator–prey systems (the reciprocal influences of predator and prey population changes) is also important to understand natural population balances as well as the successes or failures of biocontrol introductions (see Chapter 5, Forest Insect Population Dynamics).

6.5.1 Prey Finding

Visual cues (shape, size, movement, colour -at least for birds) are often used by vertebrate predators. Visual stimuli alone suffice in some cases, as illustrated by bird

predation studies relying only on artificial caterpillars made of plasticine (Seifert et al. 2015). *Public information* conveyed by the sight of other individuals in the act of feeding is another important visual stimulus, described in particular for birds (Danchin et al. 2004). Some birds also use olfactory cues when foraging. The great tit, *Parus major*, has been shown experimentally to orient to apple trees infested by the winter moth, *Operophtera brumata*, following semiochemicals released by the attacked plants but not by uninfested trees (Amo et al. 2013). Olfactory cues are used by a large range of other natural enemies, from cruising nematodes to insect predators. Small mammals detect insect cocoons in the ground by their odour (Holling 1959a). The checkered beetle *Thanasimus formicarius* has an adult life protracted over several months and thus needs to feed on several successive prey species with shorter life cycles. It has antennal receptor cells keyed to a vast number of bark beetle pheromones and host volatiles (Tømmerås 1985), and responds to the pheromones of 27 bark-beetle species, attacking either conifers or broadleaves (Warzée et al. 2006). Once on the trees under attack, it feeds on the landing bark beetles, oviposits on the bark, and its larvae enter the bark-beetle galleries where they feed on any insect inside, including conspecifics. Conversely, the monospecific *Rhizophagus grandis* locates its only prey, *D. micans*, with amazing accuracy, using a very attractive and discriminatory mixture of tree-produced monoterpenes and oxygenated monoterpenes produced by the prey (Grégoire et al. 1992). In Belgium, *D. micans* is very sparsely distributed in most spruce stands (1–5 brood systems per ha), but 90% of these broods are eventually colonised by the predators. This accurate and specific capacity to locate the host is certainly one of the major reasons explaining the high success of classical biological control (see Sect. 6.6.5) of *D. micans* using this predator (Grégoire 1988; Kenis et al. 2004). Parasitoids respond to a variety of olfactory cues, depending on the life stage they parasitise. Parasitoids of adult bark beetles, such as the Pteromalid wasp *Tomicobia* spp., respond to pheromones and oviposit in the landing hosts. Egg parasitoids use a variety of cues: sex-, anti-aphrodisiac- or aggregation pheromones, or volatiles emitted by host plants and triggered by herbivore oviposition (reviews by Fatouros et al. 2008; Hilker and Fatouros 2015). Some species among the Braconidae and the Trichogrammatidae even use phoresy on fertilised host females to make sure they are present when the eggs are laid (Fatouros et al. 2005). It has long been debated how parasitoids attacking bark-beetle late larval instars locate their hosts. Mills et al. (1991), studying *Coeloides bostrychorum* parasitising *Ips typographus*, developed an elegant series of experiments involving an infra-red scanner, thermistor probes, cellulose or wax barriers, and freezing infested logs before their exposure to parasitoids, and concluded that chemical cues and not sounds, vibrations or heat mediate host location by *C. bostrychorum*. A review of semiochemical-assisted prey location in tritrophic systems has been published by Vet and Dicke (1992).

6.5.2 Prey Exploitation and the Components of Predation

Once a prey has been located, important choices must be made. The females of *haplodiploid* parasitoids can select the sex of each egg by deciding whether to fertilise it (opening their *spermatheca*, resulting in a diploid female) or to lay it unfertilised (resulting in a haploid male). The choice often depends on the host's size, a larger host producing a larger parasitoid. As dispersal capacity, longevity and fecundity are often positively correlated with body size, in many cases, large hosts are devoted to the female offspring, which will have to disperse further and live longer than males and produce eggs themselves. Insect prey are not passive participants in parasitoid-prey interactions and attempt to defend themselves (e.g. by encapsulating eggs with melanocytes). Some parasitoid species inject a venom, and/or polydnviruses together with their eggs, which inhibit the host's defenses (Strand and Burke 2013). Remarkably it appears that herbivores that have been injected with viruses and venom by their parasitoids, elicit different volatiles from their host plants than uninfested herbivores and hyperparasitoids appear to be able to exploit this information for host location (Zhu et al. 2018). Other information used by natural enemies include oviposition stimuli or inhibitors, i.e. chemicals that indicate the availability of prey for the predator's offspring or, on the contrary, the local abundance of conspecific predators and hence a risk of intraspecific competition. Once in the brood chamber of its prey, *Rhizophagus grandis* uses chemical information from its prey to assess the size of the local prey population and adjust oviposition accordingly (more prey produce more semiochemicals and induce higher oviposition). Conversely, the presence of conspecific predators leads to reduced egg laying (Dohet and Grégoire 2017).

The mechanisms described above explain individual predator success in prey location and exploitation. Together with other interactions with the biotic (e.g. competition, hyperparasitism, host plant resistance) and abiotic (e.g. temperature, humidity, thermoperiod, photoperiod) environment, they constitute the basic components of the complex interactions that occur at the population level. These interactions grow in complexity when several successive predator and prey generations are considered. Spatial constraints lead to additional levels of complexity, for example when populations are constituted by smaller units (metapopulations) more or less loosely connected together in fragmented habitats. The quantitative population changes across space and time resulting from this whole set of interactions generally exerts a profound influence on the population dynamics of forest insects as a whole (see Chapter 5).

It is striking that much of the early pioneering work on these predator-prey relationships has been based on forest insects. Tinbergen (1960), studying the predation behaviour of great tits (*Parus major*) on forest insects in Dutch pine forests, quantified how the frequency and size of the various available prey influence predation rates. He introduced the concept of *searching image*: vertebrate predators learn from experience and, with time, improve their efficiency at finding the most abundant or most preferred prey. This concept has since influenced the behavioural sciences (Davies

et al. 2012). The seminal work by Holling (1959a, 1959b, 1961) used field and laboratory studies to quantify the prey consumption of several small predatory mammals in response to various cocoon densities of the European pine sawfly *Neodiprion sertifer*. This work also measured their responses when more or less palatable alternate food resources (respectively sunflower seeds or dog biscuits) were mixed with the cocoons. Holling (1959b) also used experiments with a blinded human subject asked to collect small sandpaper discs deployed at various densities on a table, to develop what has been since named the *Holling's disc equation*. This work described three possible quantitative responses of predators to increasing prey density (*functional responses*): (i) a theoretical, linear one (*type I functional response*) with a constant predation rate irrespective of prey density, (ii) a second type of response, with decreasing predation rates levelling off at a certain prey density (*type II functional response*), described by *Holling's disc equation*, and distinguishing between *searching time* which would decrease with increasing prey density, and a fixed *handling time* needed for either prey consumption or oviposition; and (iii) a sigmoid *type III functional response* that has been observed among vertebrate predators that learn (e.g. develop a searching image). In addition to these individual functional responses, predator populations also show *numerical responses* to prey density. They tend to aggregate and/or reproduce more abundantly in sites of higher prey density (respectively *aggregative-* and *reproductive numerical responses*). These two types of behaviours (functional and numerical responses) are further influenced by predator interactions that increase in frequency as predator density increases. These intraspecific interactions between predators can have adverse effects on individual predation and lead to different predator-dependent functional response models (see discussion in Skalski and Gilliam 2001). When multiple generations are considered, it becomes also possible to detect delayed impacts which would not occur immediately but at the following prey generation. For example, Turchin et al. (1999) suggested that the population cycles of the Southern pine beetle, *Dendroctonus frontalis*, are driven by a delayed density-dependent impact of natural enemies, in particular of the predatory checkered beetle, *Thanasimus dubius*.

Insects have developed many resistance mechanisms. *Immunity mechanisms* include phagocytosis or encapsulation by hemocytes (also valid for larger bodies such as parasitoid eggs), enzymatic proteolysis, and the synthesis by the fat body or the hemocytes of antimicrobial peptides that protect insects against viruses (Sparks et al. 2008), bacteria and fungi (Gillespie et al. 1997), and nematodes (Castillo et al., 2011). *Chemical defense* is common in insects and includes compounds sequestered from larval and adult diet or produced *de novo* (Pasteels et al. 1983). For example, larvae of Diprionid sawflies regurgitate monoterpene droplets collected from the host tree (Eisner et al., 1974), the nature of which can vary according to host tree species (Codella and Raffa 1995). Leaf beetle adults and larvae secrete defensive chemicals, often sequestered from their host plant (Laurent et al. 2005). Some caterpillars such as those of the processionary moths (*Thaumetopoea* spp.) or of the Siberian moth (*Dendrolimus sibiricus*) can project in the air hundreds of thousand minute (0.1 mm) hollow hairs containing allergenic proteins that can seriously harm vertebrate predators, although some insectivorous birds or parasitic wasps or flies do not

seem sensitive. Some species escape because they are *cryptic*, difficult to distinguish from their environment, others are *mimetic*. *Batesian mimicry* corresponds to defenseless species resembling a defended insect. Clearwings moths (Sesiidae) look like wasps, with their transparent wings and transversely striped black and yellow abdomen. *Müllerian mimics* are species that are all chemically defended but have a similar appearance, thus sharing the cost of predator learning.

A clear, ancient but still very relevant, introduction to predator–prey relationships in a forest population ecology context is provided by Varley et al. (1973).

6.6 Biological Control

6.6.1 Definition

Eilenberg et al. (2001) proposed an operative and widely followed definition of biological control (or biocontrol): “*The use of living organisms to suppress the population density or impact of a specific pest organism, making it less abundant or less damaging than it would otherwise be*”. However, Heimpel and Mills (2017) remark that this definition excludes natural control, “*the use of*” referring to manipulative control, and that, taken literally, “*living organisms*” excludes viruses as biocontrol agents.

Biocontrol can involve native or exotic natural enemies, against native or exotic prey. The introductions may occur in one point in time, followed by long-term establishment, or may need to be repeated periodically.

Four types of biological control have been identified: inoculative-, inundative-, conservation- and classical biocontrol. The first two strategies rely on the long-term mass-production of beneficials which, in most cases, can only be justified economically if there is a stable demand. They thus fit well with the needs of agriculture and the greenhouse industry but presently are usually of lesser general relevance for forest insects.

Comprehensive reviews of biological control have been published by Van Driesche and Bellows (1996), Heimpel and Mills (2017), and Hajek and Eilenberg (2018).

6.6.2 Inoculative Biological Control

This approach consists of the periodical introduction of natural enemies that establish, multiply and spread. This strategy is widely used in glasshouses where several crops are cultivated each year and the pests reappear regularly after a new crop has been started. It is sometimes used against pests with populations that fluctuate dramatically in density. Nucleopolyhedroviruses (NPVs) are regularly used against the spongy

moth, *Lymantria dispar*, the Douglas-fir tussock moth, *Orgyia pseudotsugata* and various sawflies (*Neodiprion sertifer*, *N. lecontei*) (van Frankenhuyzen et al. 2007). Entomopathogenic nematodes are used to kill the immature stages of the pine weevil, *Hyllobius abietis* in the tree stumps where they develop (Dillon et al. 2006). Natural enemies and pests can be either exotic or native.

6.6.3 *Inundative Biological Control*

This type of biological control is based on the release of large numbers of natural enemies that should exert control immediately. No establishment or only limited reproduction is expected. For example, mass-releases of *Trichogramma* wasps (egg parasitoids) are made in maize fields at the time of oviposition of the maize corn borer, *Ostrinia nubilalis* (Razinger et al. 2016). There might be one or two wasp generations produced during this period if moth oviposition is protracted but the natural enemies disappear afterward. In the forest environment, inundative releases of *Bacillus thuringiensis* subsp. *kurstaki* (Btk) have been successful against the spruce budworm, *Choristoneura fumiferana* in Canada and the USA (van Frankenhuyzen et al. 2007). Target mortality is not caused by the bacteria but by the toxins liberated by the crystals in the released sporangia, and there is no evidence that the bacteria reproduce (Garczynski and Siegel 2007). Therefore, it could be argued that Bt is a biopesticide rather than a biocontrol agent. Natural enemies and pests can be either exotic or native.

6.6.4 *Conservation Biological Control*

This strategy includes habitat manipulation in order to maintain or increase the abundance of native natural enemies. The provision of alternate hosts or prey on alternate host plants, alternate food sources (e.g. pollen- or nectar-producing plants to sustain adult parasitoids; acorns for polyphagous mammals—see Sect. 6.2.1), pupation sites for insects (see Sect. 6.4), nesting sites for birds, or overwintering shelters, have all been used as components of conservation biocontrol. Improving inter-patch connectivity by creating vegetation corridors can also be a component of conservation biological control. Brockerhoff et al. (2008) remarked that, although plantation forests are poorer habitats than natural forests, they still provide suitable habitats to many species. Jactel and Brockerhoff (2007) showed in a meta-analysis of 119 studies that herbivory by oligophagous insects is significantly reduced in mixed forest as compared to monospecific stands, but the respective roles of host-tree dilution and natural enemy enhancement are unclear. Conservation biocontrol is thus very relevant for the control of forest pests but at the moment, we are still lacking most of the knowledge and mastery of ecosystem functioning necessary for a full use of this strategy.

6.6.5 *Classical Biological Control*

This approach usually targets exotic pests, often pests of woody plants, and involves the introduction of natural enemies collected in the area of origin of the target pests. There are cases, however, where exotic natural enemies were successfully introduced against native pests, or against exotic species with which they are not associated in their area of origin. These latter cases belong to a subcategory, “new association classical biological control”. Once established, the biocontrol agent usually remains permanently present and does not need to be reintroduced.

Since the first successful introduction of two exotic natural enemies from Australia (the coccinellid beetle, *Rodolia cardinalis*, and the tachinid fly, *Cryptochetum iceryae*: Caltagirone and Doust (1989)) into California in 1898 against an exotic pest of citrus, the cottony cushion scale *Icerya purchasi*, 6,158 introductions involving 2,384 exotic insect natural enemy species have been attempted against 588 exotic insect pests between 1886 and 2010 (Cock et al. 2016). Kenis et al. (2017) calculated that ca. 55% of these introductions targeted pests of woody plants, with an establishment rate of 37% vs. 30% with other pests, and a 34% success rate (i.e. efficient pest control) vs. 24% with other pests.

A comprehensive worldwide catalogue of the introductions of nematodes and pathogens against insects and mites exists (Hajek et al. 2016). Among 131 programmes using exotic pathogens and nematodes against 76 insect species and 3 mites, 75 programmes (57%) targeted woody plant pests (Hajek et al. 2007), with an establishment rate above 60% vs. to 40% for all other habitats. The basis for the higher rates of establishment and control on woody plants is hypothesized to be the favourable environment provided by forests (see Sect. 6.4), as well as the technical and regulatory obstacles to apply control methods widely used in agriculture, such as insecticide treatments, often prohibited and anyway often useless in the forest environment, or mating disruption which often needs to be applied over vast areas in order to prevent mated females from the neighbourhood to recolonise the treated zone.

The rationale behind this successful approach is that exotic species become pests in new areas because the coevolved natural enemies that control them in their area of origin were not also introduced. Therefore, the first step of any classical biological programme is to *identify the origin of the pest*, using literature records, museum collections, molecular phylogeography, etc.

Then, *foreign exploration* can start, in order to find natural enemies that could be taken to the area newly colonised by the pest. Because the pest is sometimes very tightly controlled by natural enemies in its original range, simply finding the pest can be difficult, not to mention collecting sufficiently high numbers. One approach to circumvent this difficulty is to rear large numbers of the host/pest in the laboratory and deploy them in the field in the area of origin in order to induce attacks from local natural enemies that could be reared out of the exposed insects. This approach was followed by Mills and Nealis (1992) who, searching for natural enemies to introduce in Canada for the biological control of *Lymantria dispar*, reared out a Tachinid

parasitoid fly, *Aphantorhaphopsis samarensis* from spongy moth larvae exposed in European sites where the moth populations densities were very low. Another example concerns the Asian longhorned beetle, *Anoplophora glabripennis*, an introduced pest in North America and Europe, which is common in parts of China but rare in others. Adult beetles were collected in the field in China, allowed to oviposit in willow logs in the laboratory, and the logs hung from trees in areas of low density to attract natural enemies. Twelve species, many new to science, were recovered using this method (Li et al. 2020).

The more individuals are collected from as many origins as possible, the better, because this increases the diversity of the released biocontrol agents and their capacity to adapt to their new habitats. However, the successful introduction of *R. cardinalis* consisted of only 129 individuals, which successfully established (Caltagirone and Doutt 1989). Sometimes, individuals of different strains differ in their relationships to the prey. For example, an English strain of the ichneumonid parasitoid *Mesoleius tenthredinis* introduced in Canada to control *Pristiphora erichsoni*, proved susceptible to egg encapsulation by its host (Muldrew 1953), while a Bavarian strain released later was not encapsulated (Ives and Muldrew 1984). Similarly, while most strains of the nematode *Deladenus siridicicola* sterilize female *Sirex noctilio* (see Sect. 6.3), a strain unintentionally introduced in northeastern North America does not fully sterilize its hosts, resulting in less efficient biocontrol (Kroll et al. 2013).

After collection, natural enemies must then either be cultured locally or sent to the country of destination, to be reproduced, further identified (if necessary using molecular methods) and tested for non-target effects. Most countries will not allow the release of generalist natural enemies that will attack non-target organisms native to the country of release. All these steps are usually placed under strict administrative control in both the countries of origin and of destination. The candidate for release must then be kept in a quarantine facility (a high security laboratory with rigorous procedures accounting for all movements in and out) and reared for several generations in order to make sure that they are free of diseases or hyperparasites (hyperparasites: see Box 6.1). They must also be tested for their impact not only on the target species, but also on non-target organisms. Finally, if release is authorised, they must be mass-produced and submitted to quality control tests.

Usually, the higher the numbers released, the higher the chances of establishment. Impact assessments, including assuring that non-target attack is not occurring, must theoretically be performed at a later stage, but funding does not always allow for this last step.

One important prerequisite to biocontrol is to assess in advance potential environmental risks connected to the release of an exotic organism in a new environment. Past experience has repeatedly demonstrated that, once established, poorly selected biocontrol agents can become pests on their own. In Massachusetts, Boettner et al. (2000) found that a generalist parasitoid tachinid fly, *Compsilura concinnata*, introduced to North America in 1906 against different targets (including the spongy moth and the brown tailed moth), were heavily parasitizing three species of native saturniid moths, and they suggest that *C. concinnata* could be responsible for the observed local decline of silk moths. Another example is the recent expansion worldwide of

the Asian lady beetle, *Harmonia axyridis*, mass-released in many countries in the world and which now exerts intense intraguild predation upon other aphidophagous species (Roy et al. 2012). A review of non-target impacts of classical biocontrol has been published by Myers and Cory (2017).

The many cases of successful or partly successful classical biocontrol of forest pests have been reviewed by Kenis et al. (2017), Hajek et al. (2007) and Hajek and van Frankenhuyzen (2017) and some examples are developed in more details by Van Driesche and Bellows (1996), Hajek and Eilenberg (2018), Van Driesche et al. (2010), Van Driesche and Reardon (2014) and MacQuarrie et al. (2016). A recent example is the introduction in Italy of the parasitoid wasp *Torymus sinensis* imported from Japan against the introduced Asian chestnut gall wasp, *Dryocosmus kuriphilus*, and which resulted in excellent control after 7–8 years (Ferracini et al. 2018). On the basis of this success *T. sinensis* has also been introduced in Croatia, France, Hungary, Portugal, Slovenia, Spain, and Turkey. Another recent example of promising classical biocontrol is the introduction in North America of exotic parasitoids against the emerald ash borer, *Agrilus planipennis* (Box 6.2).

BOX 6.2—Classical biological control of the emerald ash borer in North America

In response to the invasion of the United States by the destructive emerald ash borer (EAB), *Agrilus planipennis*, scientists from the U.S. and China, Korea, and Russia collaborated to discover promising natural enemies that could be released in a classical biological control program. Potential biocontrol agents were imported into quarantine and host specificity testing was conducted. In 2007, permits were issued for the release of three of the agents: two larval parasitoids, *Spathius agrili* (Hymenoptera: Braconidae) and *Tetrastichus planipennisi* (Hymenoptera: Eulophidae), and the egg parasitoid *Oobius agrili* (Hymenoptera: Encyrtidae). Releases began in the Midwest and have expanded to 30 states as the EAB population has spread throughout the country. Follow-up monitoring shows that *T. planipennisi* is establishing well in 18 mostly northern states, and although *O. agrili* is small and difficult to recover, it too seems to be establishing in 15 states. *Spathius agrili* populations have been recovered for a year or two after release, but populations do not persist in the north. Research on the phenology of EAB and its parasitoids (Jones et al. 2020) showed that *S. agrili* is better synchronized with EAB populations that have a one-year lifecycle (like what is found in the southern United States) and *T. planipennisi* does better where EAB has a two-year lifecycle (as in the northern United States). Gould et al. (2020) developed a model of EAB development based on summer temperatures that predicts the likelihood of parasitoid establishment throughout the country based on the availability of EAB larvae in the spring. A large parasitoid like *S. agrili* is needed in the northern United States, however, because *T. planipennisi* has a short ovipositor and can only parasitize EAB in branches less than 11 cm in diameter (Abell et al. 2012).

Scientists have discovered a new EAB parasitoid in the genus *Spathius*, *S. galinae*, from Russia. Climate matching indicates a better fit for the northern U.S. and early results indicate that this parasitoid is establishing well (Duan et al. 2019). The ultimate goal of releasing biocontrol agents is not just to get them established, but for the parasitoids to reduce EAB population density and ultimately improve the health of ash trees. Recent studies of the next generation of ash growing in sites where *T. planipennisi* has established indicate that this parasitoid, combined with predation by native woodpeckers, has the potential to maintain EAB at a low density following an outbreak (Duan et al. 2017). Work is underway to discover which parasitoids are best suited for the variety of climate conditions in the United States, to quantify the role that *O. agrili* is playing where it has established, and how to integrate the use of insecticides and biological control to save mature trees in urban and natural forests.

6.7 Synthesis and Perspectives

The rich and rather stable conditions generally provided by forest ecosystems and woody plants in general favor complex food webs where assemblages of herbivorous insects coexist with predators, parasitoids, nematodes and pathogens. In most cases, particularly when the forest itself is diversified in tree species and ages, the herbivore populations remain at low levels, with little economic or environmental impact. This balance can be upset when the status of some of the components of these communities change, for example when climatic factors (e.g. droughts, heat waves, storms) weaken the trees, or when anthropogenic actions (e.g. clear cuts, plantations, fire control) modify tree composition and resistance, or when an introduced hyperparasitoid modifies the impact of a natural enemy. Changes in tree resistance or tolerance to herbivores, or relief from natural enemy pressure, can allow herbivores to build up larger populations and acquire pest status, temporarily or permanently. The introduction of exotic herbivores constitutes another type of perturbation. Kept in check by natural enemies or host resistance in their areas of origin, some invasive species can severely harm the newly colonized forests, sometimes even threatening the survival of whole tree taxa. As illustrated above (see Sect. 6.6.5), classical biological control has often provided long-term and sustainable solutions against exotic pests.

The intricate relationships between the various species interacting in the forest environment provide rich ground for basic and applied biological and ecological studies, and for their application to forest management. However, our understanding of these systems is still extremely incomplete and there will even be levels of complexity that we shall never grasp fully, even though research regularly brings forward new and exciting results.

References

- Abell KJ, Duan JJ, Bauer L, Lelito JP, Van Driesche RG (2012) The effect of bark thickness on host partitioning between *Tetrastichus planipennis* (Hymen: Eulophidae) and *Atanycolus* spp. (Hymen: Braconidae), two parasitoids of emerald ash borer (Coleop: Buprestidae). *Biol Control* 63:320–325
- Amo L, Jansen JJ, Van Dam NM, Dicke M, Visser ME (2013) Birds exploit herbivore-induced plant volatiles to locate herbivorous prey. *Ecol Lett* 16(11):1348–1355. <https://doi.org/10.1111/ele.12177>
- Boddy L (2016) Interactions with Humans and Other Animals. In: Watkinson SC, Boddy L, Money NP (eds) *The Fungi* (Third Edition). Academic Press, pp 293–336, 466 pp
- Boeing AL, Nichols E, Metzger JP (2017) Effects of landscape structure on avian-mediated insect pest control services: a review. *Landscape Ecol* 32(5):1–14. <https://doi.org/10.1007/s10980-017-0503-1>
- Boettner GH, Elkinton JS, Boettner CJ (2000) Effects of biological control introduction on three nontarget native species of saturniid moths. *Conserv Biol* 14:1798–1806
- Brockerhoff EG, Jactel H, Parrotta JA, Quine CP, Sayer J (2008) Plantation forests and biodiversity: oxymoron or opportunity? *Biodivers Conserv* 17(5):925–951
- Buckner CH (1966) The role of vertebrate predators in the biological control of forest insects. *Annu Rev Entomol* 11(1):449–470
- Caltagirone LE, Doutt RL (1989) The history of the vedalia beetle importation to California and its impact on the development of biological control. *Annu Rev Entomol* 34:1–16
- Castillo JC, Reynolds SE, Eleftherianos I (2011) Insect immune responses to nematode parasites. *Trends Parasitol* 27(12):537–547
- Cock MJ, Murphy ST, Kairo MT, Thompson E, Murphy RJ, Francis AW (2016) Trends in the classical biological control of insect pests by insects: an update of the BIOCOT database. *Biocontrol* 61(4):349–363
- Codella SG, Raffa KF (1995) Host plant influence on chemical defense in conifer sawflies (Hymenoptera: Diprionidae). *Oecol* 104(1):1–11
- Cronin JT, Reeve JD, Wilkens R, Turchin P (2000) The pattern and range of movement of a checkered beetle predator relative to its bark beetle prey. *Oikos* 90(1):127–138
- Cronin JT, Reeve JD (2005) Host-parasitoid spatial ecology: a plea for a landscape-level synthesis. *Proc R Soc Lond B Biol Sci* 272:2225–2235
- Cruz YP (1981) A sterile defender morph in a polyembryonic hymenopterous parasite. *Nature* 294(5840):446
- Danchin É, Giraldeau LA, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. *Science* 305(5683):487–491
- Davies NB, Krebs JR, West SA (2012) *An introduction to behavioural ecology*. John Wiley & Sons
- Dillon AB, Ward D, Downes MJ, Griffin CT (2006) Suppression of the large pine weevil *Hylobius abietis* (L.) (Coleoptera: Curculionidae) in pine stumps by entomopathogenic nematodes with different foraging strategies. *Biol Control* 38(2):217–226
- Dodds KJ, Graber C, Stephen FM (2001) Facultative intraguild predation by larval Cerambycidae (Coleoptera) on bark beetle larvae (Coleoptera: Scolytidae). *Environ Entomol* 30(1):17–22
- Dohet L, Grégoire J-C (2017) Is prey specificity constrained by geography? Semiochemically mediated oviposition in *Rhizophagus grandis* (Coleoptera: Monotomidae) with its specific prey, *Dendroctonus micans* (Coleoptera: Curculionidae: Scolytinae), and with exotic *Dendroctonus* species. *J Chem Ecol* 43(8):778–793. <https://doi.org/10.1007/s10886-017-0869-1>
- Duan JJ, Van Driesche RG, Crandall RS, Schmude JM, Rutledge CE, Slager BH, Gould JR, Elkinton JS (2019) Establishment and early impact of *Spathius galinae* (Hymenoptera: Braconidae) on emerald ash borer (Coleoptera: Buprestidae) in the northeastern United States. *J Econ Entomol* 112:2121–2130
- Duan JJ, Bauer LS, Van Driesche RG (2017) Emerald ash borer biocontrol in ash saplings: the potential for early stage recovery of North American ash trees. *For Ecol Manage* 394:64–72

- Eilenberg J, Hajek A, Lomer C (2001) Suggestions for unifying the terminology in biological control. *Biocontrol* 46:387–400
- Eisner T, Johnessee JS, Carrel J, Hendry LB, Meinwald J (1974) Defensive use by an insect of a plant resin. *Science* 184:996–999
- Elkinton JS, Healy WM, Buonaccorsi JP, Boettner GH, Hazzard AM, Smith HR, Liebhold AM (1996) Interactions among gypsy moths, white-footed mice, and acorns. *Ecol* 77(8):2332–2342
- Elkinton JS, Liebhold AM (1990) Population dynamics of gypsy moth in North America. *Annu Rev Entomol* 35(1):571–596
- Eveleigh ES, McCann KS, McCarthy PC, Pollock SJ, Lucarotti CJ, Morin B et al (2007) Fluctuations in density of an outbreak species drive diversity cascades in food webs. *Proc Natl Acad Sci USA* 104:16976–16981
- Fatouros NE, Dicke M, Mumm R, Meiners T, Hilker M (2008) Foraging behavior of egg parasitoids exploiting chemical information. *Behav Ecol* 19(3):677–689
- Fatouros NE, Huigens ME, van Loon JJ, Dicke M, Hilker M (2005) Chemical communication: butterfly anti-aphrodisiac lures parasitic wasps. *Nature* 433(7027):704
- Ferracini C, Ferrari E, Pontini M, Saladini MA, Alma A (2018) Effectiveness of *Torymus sinensis*: a successful long-term control of the Asian chestnut gall wasp in Italy. *J Pest Sci* 1–7
- Frost C, Didham R, Rand T, Peralta G, Tylianakis J (2015) Community-level net spillover of natural enemies from managed to natural forest. *Ecol* 96(1):193–202
- Garczynski SF, Siegel JP (2007) Bacteria. In: Lacey LA, Kaya HK (eds) Field manual of techniques in invertebrate pathology: application and evaluation of pathogens for control of insects and other invertebrate pests. Springer Science & Business Media, pp 175–197
- Gillespie JP, Kanost MR, Trenczek T (1997) Biological mediators of insect immunity. *Annu Rev Entomol* 42(1):611–643
- Giron D, Dunn DW, Hardy IC, Strand MR (2004) Aggression by polyembryonic wasp soldiers correlates with kinship but not resource competition. *Nature* 430(7000):676
- Godfray HCJ (1994) Parasitoids: behavioral and evolutionary ecology. Princeton University Press, pp 473
- Gould JR, Warden ML, Slager BH, Murphy TC (2020) Host overwintering phenology and climate change influence the establishment of *Tetrastichus planipennis*, a larval parasitoid introduced for biocontrol of the emerald ash borer. *J Econ Entomol*. <https://doi.org/10.1093/jee/toaa217>
- Grégoire JC (1988) The Greater European Spruce Beetle, *Dendroctonus micans* (Kug.). In: A.A. Berryman (ed) Population dynamics of forest insects, Plenum, New York, pp 455–478, 604 pp
- Grégoire JC, Couillien D, Krebber R, König WA, Meyer H, Francke W (1992) Orientation of *Rhizophagus grandis* (Coleoptera: Rhizophagidae) to oxygenated monoterpenes in a species-specific predator-prey relationship. *Chemoecology* 3:14–18
- Hajek AE, Gardescu S, Delalibera I Jr (2016) Classical biological control of insects and mites: a worldwide catalogue of pathogen and nematode introductions. USDA Forest Service. FHTET-2016–06.
- Hajek AE, McManus ML, Delalibera I Jr (2007) A review of introductions of pathogens and nematodes for classical biological control of insects and mites. *Biol Control* 41:1–13
- Hajek AE, Eilenberg J (2018) Natural enemies: an introduction to biological control. Cambridge University Press, 246 pp
- Hajek AE, van Frankenhuyzen K (2017) Use of entomopathogens against forest pests. In microbial control of insect and mite pests, pp 313–330
- Heimpel GE, Mills NJ (2017) Biological control: ecology and applications. Cambridge University Press, Cambridge, pp xii + 380
- Hilker M, Fatouros NE (2015) Plant responses to insect egg deposition. *Annu Rev Entomol* 60:493–515
- Holling CS (1959a) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can Entomol* 91(5):293–320
- Holling CS (1959b) Some characteristics of simple types of predation and parasitism. *Can Entomol* 91(7):385–398

- Holling CS (1961) Principles of insect predation. *Annu Rev Entomol* 6(1):163–182
- Hougaard E, Grégoire J-C (2000) Spruce stands provide natural food sources to adult hymenopteran parasitoids of bark beetles. *Entomol Exp Appl* 96:253–263
- Huang N, Enkegaard A (2010) Predation capacity and prey preference of *Chrysoperla carnea* on *Pieris brassicae*. *Biocontrol* 55(3):379–385
- Ives WGH, Muldrew JA (1984) *Pristiphora erichsonii* (Hartig), larch sawfly (Hymenoptera: Tenthredinidae). In: Kelleher JS, Hulme MA (eds) Biological control programmes against insects and weeds in Canada: 1969–1980. Commonwealth Agricultural Bureaux, Farnham Royal, United Kingdom, pp 369–380
- Jactel H, Brockerhoff EG (2007) Tree diversity reduces herbivory by forest insects. *Ecol Lett* 10(9):835–848
- Jennings DE, Duan JJ, Bauer LS, Schmude JM, Wetherington MT, Shrewsbury PM (2016) Temporal dynamics of woodpecker predation on emerald ash borer (*Agrilus planipennis*) in the northeastern U.S.A. *Agric For Entomol* 18(2):174–181. <https://doi.org/10.1111/afe.12142>
- Jervis MA (ed) (2012) Insect natural enemies: practical approaches to their study and evaluation. Springer Science & Business Media, p 491
- Jones MI, Gould JR, Mahon HJ, Fierke MK (2020) Phenology of emerald ash borer (Coleoptera: Buprestidae) and its introduced larval parasitoids in the northeastern United States. *J Econ Entomol* 113:622–632
- Karp DS, Mendenhall CD, Sandí RF, Chaumont N, Ehrlich PR, Hadly EA, Daily GC (2013) Forest bolsters bird abundance, pest control and coffee yield. *Ecol Lett* 16(11):1339–1347. <https://doi.org/10.1111/ele.12173>
- Kaya HK, Gaugler R (1993) Entomopathogenic Nematodes. *Annu Rev Entomol* 38(1):181–206
- Keenan RJ, Reams GA, Achard F, de Freitas JV, Grainger A, Lindquist E (2015) Dynamics of global forest area: results from the FAO Global Forest Resources Assessment 2015. *For Ecol Manage* 352:9–20
- Kenis M, Hurley BP, Hajek AE, Cock MJW (2017) Classical biological control of insect pests of trees: facts and figures. *Biol Invasions* 19(11):3401–3417. <https://doi.org/10.1007/s10530-017-1414-4>
- Kenis M, Wermelinger B, Grégoire JC (2004) Research on parasitoids and predators of Scolytidae in living trees in Europe—a review. In: Lieutier F, Day K, Battisti A, Grégoire JC, Evans H (eds) Bark and wood boring insects in living trees in Europe, a Synthesis. Kluwer, Dordrecht, pp 237–290, 583 pp
- Kroll SA, Hajek AE, Morris EE, Long SJ (2013) Parasitism of *Sirex noctilio* by non-sterilizing *Deladenus siricidicola* in northeastern North America. *Biol Control* 67(2):203–211
- Lacey LA (ed) (2016) Microbial control of insect and mite pests: from theory to practice. Academic Press.
- Lacey LA, Grzywacz D, Shapiro-Ilan DI, Frutos R, Brownbridge M, Goettel MS (2015) Insect pathogens as biological control agents: back to the future. *J Invertebr Pathol* 132:1–41
- Lacey LA, Kaya HK (eds) (2007) Field manual of techniques in invertebrate pathology: application and evaluation of pathogens for control of insects and other invertebrate pests. Springer Science & Business Media
- Laurent P, Braekman JC, Daloze D (2005) Insect chemical defense. In: Schulz S. (eds) The chemistry of pheromones and other semiochemicals II. Topics in current chemistry, vol 240. Springer, Berlin, Heidelberg
- Leius K (1963) Effects of pollen on fecundity and longevity of adult *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae). *Can Entomol* 95:202–207
- Leius K (1961) Influence of various foods on fecundity and longevity of adults *Scambus buolianae* (Htg.) (Hymenoptera: Ichneumonidae). *Can Entomol* 93:1079–1084
- Li F, Zhang YL, Wang XY, Cao LM, Yang ZQ, Gould JR, Duan JJ (2020) Discovery of Parasitoids of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) and their seasonal abundance in China using sentinel Host Eggs and Larvae. *J Econ Entomol* 113(4):1656–1665. <https://doi.org/10.1093/jee/toaa068>

- Liebhold AM, Raffa KF, Diss AL (2005) Forest type affects predation on gypsy moth pupae. *Agric for Entomol* 7(3):179–185
- Liebhold AM, Elkinton J, Williams D, Muzika RM (2000) What causes outbreaks of the gypsy moth in North America? *Popul Ecol* 42(3):257–266
- Limburg DD, Rosenheim JA (2001) Extrafloral nectar consumption and its influence on survival and development of an omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). *Environ Entomol* 30(3):595–604
- MacQuarrie C, Lyons D, Lukas Seehausen M, Smith S (2016) A history of biological control in Canadian forests, 1882–2014. *Can Entomol* 148(S1):S239–S269
- Mathews PL, Stephen FM (1997) Effect of artificial diet on longevity of adult parasitoids of *Dendroctonus frontalis* (Coleoptera: Scolytidae). *Environ Entomol* 26(4):961–965
- Mills NJ, Krüger K, Schlup J (1991) Short-range host location mechanisms of bark beetle parasitoids. *J Appl Entomol* 111(1–5):33–43
- Mills NJ, Nealis VG (1992) European field collections and Canadian releases of *Ceranthia samarensis* (Dipt.: Tachinidae), a parasitoid of the gypsy moth. *Entomophaga* 37:181–191
- Morris RJ, Lewis OT, Godfray HCJ (2004) Experimental evidence for apparent competition in a tropical forest food web. *Nature* 428(6980):310
- Muldrew JA (1953) The natural immunity of the larch sawfly (*Pristiphora erichsonii* (Htg.) to the introduced parasite *Mesoleius tenthredinis* Morley, in Manitoba and Saskatchewan. *Can J Zool*, 31(4):313–332.
- Murfin KE, Ginete DR, Bashey F, Goodrich-Blair H (2019) Symbiont-mediated competition: *Xenorhabdus bovienii* confer an advantage to their nematode host *Steinernema affine* by killing competitor *Steinernema feltiae*. *Environ Microbiol* 21(9):3229–3243. <https://doi.org/10.1111/1462-2920.14278>
- Myers JH, Cory JS (2017) Biological control agents: invasive species or valuable solutions? In: Vilà M, Hulme P (eds) *Impact of biological invasions on ecosystem services. Invading Nature—Springer Series in Invasion Ecology*, vol 12. Springer, Cham, pp 191–202
- Paine TD, Millar JG, Bellows TS, Hanks LM, Gould JR (1993) Integrating classical biological control with plant health in the urban forest. *J Arboric* 19:125–130
- Palmer TM, Stanton ML, Young TP, Goheen JR, Pringle RM, Karban R (2008) Breakdown of an ant-plant mutualism follows the loss of large herbivores from an African savanna. *Science* 319(5860):192–195
- Pasteels JM, Grégoire JC, Rowell-Rahier M (1983) The chemical ecology of defense in arthropods. *Annu Rev Entomol* 28(1):263–289
- Poinar GO Jr (1991) Nematoda and Nematomorpha. In: Thorp JH, Covich AP (eds) *Ecology and classification of North American freshwater invertebrates*. Academic Press, San Diego, CA, pp 249–283
- Poinar GO Jr (1975) Entomogenous nematodes: a manual and host list of insect-nematode associations. E.J. Brill, Leiden, pp 317
- Pottier A (2012) La forêt des Landes de Gascogne comme patrimoine naturel? Échelles, enjeux, valeurs. PhD dissertation, Université de Pau et des Pays de l'Adour, pp 483
- Price PW, Bouton CE, Gross P, McPherson BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. *Annu Rev Ecol Syst* 11(1):41–65
- Razinger J, Vasileiadis VP, Giraud M, van Dijk W, Modic Š, Sattin M, Urek G (2016) On-farm evaluation of inundative biological control of *Ostrinia nubilalis* (Lepidoptera: Crambidae) by *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae) in three European maize-producing regions. *Pest Manag Sci* 72:246–254. <https://doi.org/10.1002/ps.4054>
- Roland J, Taylor PD (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386:710–713
- Rosenheim JA (1998) Higher-order predators and the regulation of insect herbivore populations. *Annu Rev Entomol* 43(1):421–447

- Roy HE, Adriaens T, Isaac NJB, Kenis M, Onkelinx T, San Martin G, Brown PMJ, Hautier L, Poland R, Roy DB, Comont R, Eschen R, Frost R, Zindel R, Van Vlaenderen J, Nedvěd O, Ravn HP, Grégoire JC, de Biseau JC, Maes D (2012) Invasive alien predator causes rapid declines of native European ladybirds. *Divers Distrib* 18(7):717–725. <https://doi.org/10.1111/j.1472-4642.2012.00883.x>
- Ryall KL, Fahrig L (2006) Response of predators to loss and fragmentation of prey habitat: a review of theory. *Ecol* 87(5):1086–1093
- Schoeller EN, Husseneder C, Allison JD (2012) Molecular evidence of facultative intraguild predation by *Monochamus titillator* larvae (Coleoptera: Cerambycidae) on members of the southern pine beetle guild. *Naturwissenschaften* 99(11):913–924
- Seifert CL, Lehner L, Adams M, Fiedler K (2015) Predation on artificial caterpillars is higher in countryside than near-natural forest habitat in lowland south-western Costa Rica. *J Trop Ecol* 31(3):281–284. <https://doi.org/10.1017/S0266467415000012>
- Senthil-Nathan S (2015) A review of biopesticides and their mode of action against insect pests. In *Environmental sustainability*. Springer, New Delhi, pp 49–63
- Singer MS, Clark RE, Lichter-Marck IH, Johnson ER, Mooney KA, Rodriguez-Cabal M (2017) Predatory birds and ants partition caterpillar prey by body size and diet breadth. *J Anim Ecol* 86(6):1363–1371. <https://doi.org/10.1111/1365-2656.12727>
- Skalski GT, Gilliam JF (2001) Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology* 82(11):3083–3092
- Sparks WO, Bartholomay LC, Bonning BC (2008) Insect immunity to viruses. In: Beckage NE (ed) *Insect Immunology*. Academic Press, pp 209–242, 360 p. <https://doi.org/10.1016/b978-012-373976-6.50011-2>
- Strand MR, Burke GR (2013) Polydnavirus-wasp associations: evolution, genome organization, and function. *Curr Opin Virol* 3(5):587–594
- Tinbergen L (1960) The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by song birds. *Arch. Neerl Zool* 13:265–343
- Tømmerås BA (1985) Specialization of the olfactory receptor cells in the bark beetle *Ips typographus* and its predator *Thanasimus formicarius* to bark beetle pheromones and host tree volatiles. *J Comp Physiol A* 15:335–341
- Turchin P, Taylor AD, Reeve JD (1999) Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science* 285(5430):1068–1071
- Van Driesche RG, Reardon R (eds) (2014) *The use of classical biological control to preserve forests in North America*. United States Department of Agriculture, Forest Service, Morgantown, WV, FHTET-2013-2. <https://www.fs.fed.us/foresthealth/technology/pdfs/FHTET-2013-2.pdf>
- Van Driesche RG, Bellows TS Jr (1996) *Biological Control*. Chapman and Hall, New York, p 539
- Van Driesche RG, Carruthers RI, Center T, Hoddle MS, Hough-Goldstein J, Morin L, Smith L, Wagner DL et al (2010) Classical biological control for the protection of natural ecosystems. *Biol Control Suppl* 1:S2–S33
- van Frankenhuyzen K, Reardon RC, Dubois NR (2007) Forest defoliators. In: Lacey LA, Kaya HK, (eds) *Field manual of techniques in invertebrate pathology: application and evaluation of pathogens for control of insects and other invertebrate pests*. Springer Science & Business Media, pp 481–504
- Varley GC, Gradwell GR, Hassell MP (1973). *Insect population ecology: an Analytical Approach*. Blackwell Scientific, UK
- Vet LE, Dicke M (1992) Ecology of infochemical use by natural enemies in a tritrophic context. *Annu Rev Entomol* 37(1):141–172
- Warzée N, Gilbert M, Grégoire JC (2006) Predator/prey ratios: a measure of bark-beetle population status influenced by stand composition in different French stands after the 1999 storms. *Ann for Sci* 63(3):301–308
- Wegensteiner R, Wermelinger B, Herrmann M (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In: Vega FE, Hofstetter RW (eds) *Bark Beetles. Biology and Ecology of Native and Invasive Species*. Elsevier/Academic Press, London, UK, pp 247–304

- Yousuf F, Carnegie AJ, Bashford R, Nicol HI, Gurr GM (2018) The fungal matrices of *Ophiostoma ips* hinder movement of the biocontrol nematode agent, *Deladenus siricidicola*, disrupting management of the woodwasp, *Sirex noctilio*. *Biocontrol* 63:739–749. <https://doi.org/10.1007/s10526-018-9897-1>
- Zhu F, Cusumano A, Bloem J, Weldegergis BT, Villela A, Fatouros NE, van Loon JJA, Dicke M, Harvey JA, Vogel H, Poelman EH (2018) Symbiotic polydnavirus and venom reveal parasitoid to its hyperparasitoids. *Proc Natl Acad Sci* 115(20):5205–5210

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